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Tail Length and Mutual Mate Choice in Bearded Tits (*Panurus biarmicus*)

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Abstract

Direct sexual selection via mutual mate choice can result in both sexes showing conspicuous traits. We experimentally tested whether this hypothesis can explain tail length in the bearded tit (*Panurus biarmicus*). In this species, both sexes have a long, graduated tail. Males have, however, a longer tail than females, suggesting perhaps that females are choosier than males in selecting mates. We used two choice set-ups for each sex: shortened vs. control tail individuals and elongated vs. control tail individuals. We found that direct sexual selection seems to operate differently in the two sexes. In both set-ups, females spent more time with the male with the longest tail, and they also showed sexual display behaviour only towards these males. Males spent more time with control than with short-tailed females, but they did not discriminate between control and long-tailed females. Moreover, males displayed preference towards both short- and long-tailed females. Thus, females preferred long-tailed males, whereas males did not always prefer long-tailed females. Our study suggests that mutual mate choice has played a role in the evolution of long tails in bearded tits. It also suggests that the sexual dimorphism in tail length has evolved because mate choice exerts a stronger sexual selection pressure on males than on females.

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Introduction

Two main hypotheses have been proposed to explain the presence of ornaments or conspicuous traits in both sexes (reviewed by Amundsen 2000). The correlated response hypothesis (Lande 1980, 1987; Lande and Arnold 1985) predicts that ornamental traits in females, resembling those found in males, are a genetic by-product of sexual selection favouring the traits in males. Roulin et al.

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(2001) recently showed that a genetic correlation between the sexes determines plumage traits in barn owls *Tyto alba*, constituting the first experimental evidence for such a mechanism in wild birds. Alternatively, the trait may have evolved also in females through direct sexual selection, i.e. via male mate choice and/or female contest competition (Andersson 1994; Amundsen 2000). These hypotheses are, however, not mutually exclusive. For example, reduced trait expression resulting from genetic correlation may provide the starting point for further trait exaggeration through sexual selection (Amundsen 2000).

Theory predicts that in monogamous species with biparental care not only females but also males may benefit from being choosy (Parker 1983; McNamara and Collins 1990; Crowley et al. 1991; Johnstone et al. 1996). In such species, sexual selection may thus favour conspicuous traits in both sexes (see Andersson 1994). Intersexual differences in the intensity of sexual selection may, however, lead to differences in trait expression (Trivers 1972). Furthermore, several studies have shown that sexual selection does not necessarily favour exaggerated traits (e.g. Rowland 1995; Wollerman 1998; Balmford et al. 2000).

A large number of mate choice studies have investigated the evolution of male traits (reviewed by Andersson 1994). However, relatively few studies have examined the evolution of conspicuous traits in females (Muma and Weatherhead 1989; Hill 1993; Jones and Hunter 1993, 1999; Dale and Slagsvold 1994; Cuervo et al. 1996; Amundsen et al. 1997; Roulin 1999). When sexes show similar traits, it seems likely that males and females will also assess them in a similar way if they are important cues for mate choice. Very few studies have, however, attempted to investigate male and female mate preferences simultaneously (reviewed by Andersson 1994; see also Roulin 1999).

The bearded tit (*Panurus biarmicus*) is a socially monogamous passerine with biparental care of eggs and chicks (Cramp and Perrins 1993, pp. 94 and 97). Therefore, not only female but also male mate choice can be expected (see above). Both sexes have a long graduated tail (Cramp and Perrins 1993, p. 99), a trait that is generally influenced by intersexual selection (see Andersson 1994). Males have, however, a longer tail than females (Cramp and Perrins 1993; see below), perhaps because mate choice exerts a stronger sexual selection pressure on males than on females. In this study, we experimentally tested whether mutual mate choice may explain the presence of the long graduated tail in male and female bearded tits.

Methods

Study Species and Housing Conditions

The bearded tit inhabits almost exclusively extensive reed areas (e.g. Bibby 1983). In Austria, it is restricted to the marshes around Lake Neusiedl from where we obtained our experimental birds. On average, males had longer tails than females: 88.9 ± 0.6 mm ($\bar{x} \pm$ SE) (range 84.0–101.9 mm, n = 30) vs. 82.6 ± .5 mm (range 72.0–91.7 mm, $n = 29$). Tail length corrected for body size (i.e. the residuals from a regression of tail length on tarsus length; $r^2 = 0.37$, $p < 0.0001$) also differed significantly between the sexes (*t*-test: $t = -2.10$, $p = 0.04$). It should be noted that bearded tits are sexually dimorphic also in plumage characteristics (e.g. males have bold black moustaches and under tail-coverts; Cramp and Perrins 1993, p. 88), allowing sex recognition independent of tail length.

The study was carried out during autumn and early spring in 1996 and 2000, respectively, at the Konrad Lorenz Institute in Vienna. Bearded tits usually form pairs in the autumn, but mating can occur at any time of the year because of loss of mate or divorce (e.g. Bibby 1983). We kept the birds in single-sex flocks of about eight individuals per aviary (aviary measurements: 7 m × 5 m × 3 m). The outdoor aviaries were designed to simulate the original environment (e.g. containing reed stems), and birds were fed with commercial insect food and a variety of seed types *ad libitum*. We weighed the birds (g) and recorded wing, tarsus and tail length (mm) as described by Svensson (1992). Birds tested in different years did not differ significantly in any of these measurements (t-test: females, $t < -1.14$, $p > 0.20$, $n = 29$; males, $t < -1.67$, $p > 0.10$, $n = 30$).

Tail Manipulation

We used two set-ups for male and female mate choice experiments. (1) Shortened tail set-up: to test mate preference for shortened vs. control tail individuals. Tail manipulation was done by cutting about 20 mm (shortened) or 1 mm (control) of all the feather tips (except the outer tail feathers). After the manipulation, tail length in the shortened group varied between 65.2 and 67.2 mm (males) and between 62.0 and 66.7 mm (females). In the natural population, tail feathers can be very short because of different stages of development, or sometimes even completely missing because of accidental removal or delayed moult (H. Hoi, unpubl. data). Mean tail length as well as other measurements (body mass, wing and tarsus length) did not differ significantly, neither in females nor in males, between the two groups prior to manipulation (Mann–Whitney test: $U > 24.0$, $p > 0.30$, $n = 7$ manipulated and seven control birds in each choice experiment).

(2) Elongated tail set-up: to test mate preference for elongated vs. control tail individuals. For this experiment, feather tips that were either 25 mm (elongated) or 5 mm (control) were added to the original tail feathers (except the outer tail feathers), using small amounts of a commercial super-glue. The overlapping, glued surface was 5 mm. Thus, after manipulation the tail was at least 20 mm longer in the elongated tail individuals, but it did not increase in length in control birds. In the elongated group, our treatment resulted in tail length varying between 102.9 and 109.1 mm (males) and between 95.6 and 101.3 mm (females). The maximum tail length in the natural population is 108.0 mm for males and 102.0 mm for females (H. Hoi, unpubl. data). Again, size measurements (body mass, tail, wing and tarsus length) did not differ significantly between the two groups prior to manipulation (Mann–Whitney test:

$U > 23.0$, $p > 0.20$, $n = 7$ manipulated and seven control birds in each choice experiment).

Experimental Design

Two birds (stimulus birds) of the same sex but belonging to different experimental treatments were introduced in two different small cages (1 m × 1 m × 1 m and 0.8 m × 0.4 m × 0.4 m in 1996 and 2000, respectively) 1 m apart and visually separated, and presented to the opposite sex (Fig. 1). The cages were placed in a large 'choice aviary' (5 m × 3 m × 2 m and 5 m × 2 m × 2 m in 1996 and 2000, respectively), where the choosing bird could move freely and initiate contact with the two birds presented through a wire mesh (e.g. by using perches placed identically in both cages or even sitting on the top of the cages; Fig. 1).

The stimulus birds were introduced into the cages a few hours before sunset and kept inside 1 d prior to the start of the experiment. To avoid any confounding effect of position, the location of the bird with the shortest tail was randomly assigned in each choice experiment. Female preference for male tail length was investigated for 14 females in the shortened tail set-up and for 11 females in the elongated tail set-up. Male preference for female tail length was studied for 13 different males in each set-up. Each choosing bird was used only once in the experiments. For each set-up, seven different pairs were used as stimulus birds. Thus, some of the stimulus pairs were used more than once: five pairs in the

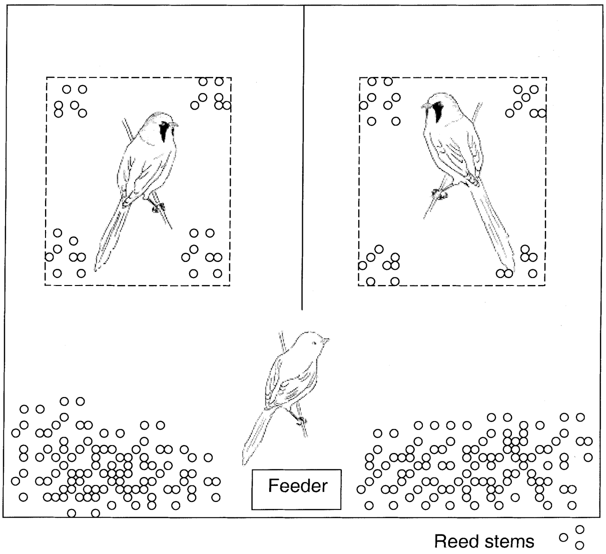

Fig. 1: The 'choice aviary'. An example of the elongated tail set-up with choosing female and two stimulus males: one with control (left) and one with elongated tail (right). The dashed lines indicate the wire mesh of the cages and the solid line between them a reed wall

female choice experiment (shortened set-up: one pair tested with four choosing females and one pair tested with five females; elongated set-up: one pair tested with three females and two pairs each tested with two females, 16 trials in total) and six pairs in the male choice experiment (in both set-ups, three pairs were each tested with three choosing males, 18 trials in total). As this may result in pseudoreplication (see Milinski 1997), we checked for dependency among these observations. First, we correlated the response behaviour towards the longest-tailed stimulus bird (i.e. control in the shortened set-up and elongated in the elongated set-up), using all pairwise combinations of data for stimulus pairs that were used more than once. This revealed a relatively weak correlation between the response behaviours in both the male (Spearman rank correlation: $r_s = -0.11, n = 18$) and the female choice experiment ($r_s = 0.02, n = 16$). Second, we calculated repeatability (r) of response behaviour, as described by Lessells and Boag (1987). This showed low repeatability in both choice experiments (male choice: $r = -0.237, F_{5,12} = 0.42, p = 0.82$; female choice: $r = -0.331, F_{4,11} = 0.32, p = 0.86$). Therefore, we treated all observations of choosing birds as statistically independent data points.

Behavioural Observations

Experimental trials were carried out by introducing the choosing bird into the ‘choice aviary’ at sunset. The next morning, three 30-min protocols were recorded at 8:00, 13:00 and 16:00 h, respectively.

We used two measures of mate choice: time spent near the stimulus birds and sexual display towards the stimulus birds. In the bearded tit, pair members typically stay very close to each other (H. Hoi, unpubl. data). Sexual display behaviour is shown by both sexes but always to the opposite sex. It consists of a close approach by the displaying individual, whereby the tail and the under tail-coverts are directed towards the potential mate for about 5–10 s (Koenig 1952; Hoi 1989).

We recorded the distance between the choosing bird and the two cages (every 30 s) and the number of displays initiated by the choosing bird (during 30 min). Following Amundsen et al. (1997), we considered that the choosing bird showed interest in the stimulus birds when this distance was between 0 and 10 cm (response area). This area constituted 19 and 12% of the total area in 1996 and 2000, respectively. By chance, a choosing bird would thus be expected to spend about 19% (1996) or 12% (2000) of the time in the response area (see Amundsen et al. 1997). The choosing birds showed, however, a clear response to the presence of a potential mate: all but one of them stayed in the response area 2–3 times more than expected by chance. The exception was one trial in the elongated set-up in 1996, where the choosing female stayed less time (10%) than expected by chance within the response area. We therefore excluded this female from the analyses. For each choosing bird tested, we used relative frequencies as approximations of the relative time spent with each of the stimulus birds (Martin and Bateson 1986).

Results

Female Preference for Male Tail Length

In both set-ups, females spent more time with the long-tailed male (Fig. 2, paired t-test: shortened tail set-up; $t = 2.65, p = 0.02, n = 14$ females, elongated tail set-up; $t = -2.48, p = 0.03, n = 10$ females).

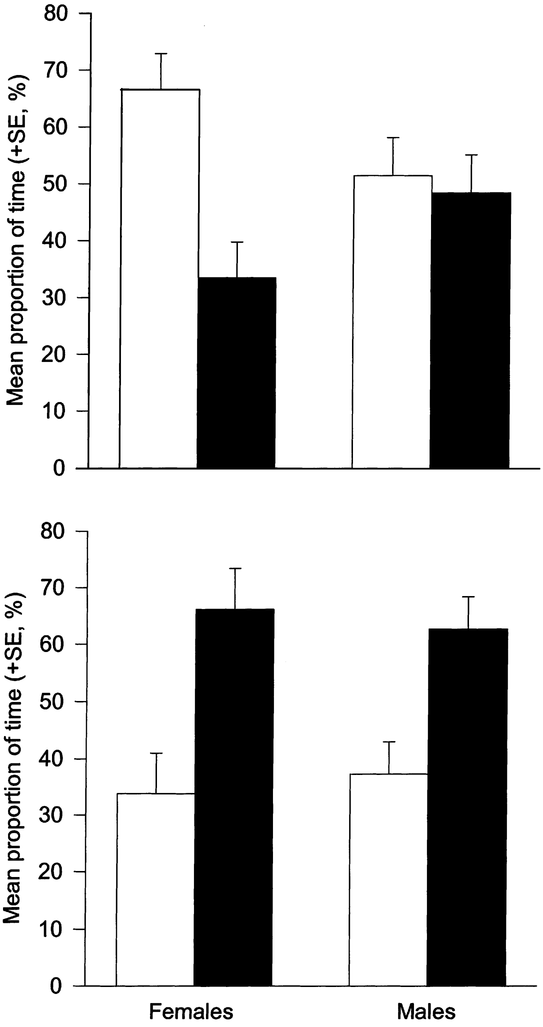

Fig. 2: Preference for tail length in female and male bearded tits. Top: elongated tail set-up, bottom: shortened tail set-up. Open bars show the proportion of time spent near the manipulated bird (elongated or shortened tail); solid bars represent time near the control bird. Sample sizes were 10 (elongated set-up) or 14 choosing females (shortened set-up) and 13 choosing males (both set-ups). See Methods for further explanations

When females showed sexual display behaviour, they only performed it towards the long-tailed male. Three out of 14 females in the shortened tail set-up performed display towards the control male (three times for each female). In the elongated tail set-up, seven out of 10 females displayed exclusively towards the male with the elongated tail ($\bar{x} \pm SE : 2.9 \pm 0.7$ displays). Thus, a significantly higher proportion of females performed sexual displays in the elongated than in the shortened tail set-up (Fisher exact test: $p = 0.04$). We found a positive correlation between the proportion of time females stayed with long-tailed males and the number of displays they performed towards them (Spearman rank correlation: $r_s = 0.78, p = 0.04, n = 7$).

Male Preference for Female Tail Length

In the shortened tail set-up, males spent significantly more time with the control than with the short-tailed female (Fig. 2, paired t-test: $t = 2.24, p = 0.04, n = 13$ males). In the elongated tail set-up, however, males spent about equal time with each female (Fig. 2, $t = -0.22, p = 0.80, n = 13$ males).

Male display behaviour also showed a different pattern than that observed in females. Overall, 22 out of 26 males displayed towards the stimulus females (12 in the shortened and 10 in the elongated set-up). Nine of these males only displayed towards one female: four out of six males displayed towards the control female in the shortened set-up, whereas one out of three males displayed towards the long-tailed female in the elongated set-up. The remaining 13 males displayed towards both females. In these cases, males appeared to distribute displays equally between the two stimulus females (shortened set-up; $46 \pm 0\%$ of displays towards the control female, $n = 6$, Wilcoxon signed ranks test: $T = 9.0, p = 0.70$, elongated set-up; $39 \pm 0\%$ of displays towards the long-tailed female, $n = 7, T = 7.0, p = 0.50$). In the elongated tail set-up, we found a negative correlation between the number of displays performed towards long-tailed females and the proportion of time males spent with them (Spearman rank correlation: $r_s = -0.74, p = 0.03, n = 8$). The relationship was also negative, although not significant, for control females in the shortened tail set-up ($r_s = -0.29, p = 0.41, n = 10$).

Discussion

We found that females preferred the long-tailed male in both set-ups. Also, males preferred control to short-tailed females, but they did not discriminate between control and long-tailed females. Our results on display behaviour corroborated female preference for long-tailed males but showed a different and more complicated pattern in males.

We did not record behaviour of the stimulus (caged) birds, so it is possible that they may have interacted acoustically or behaviourally with the choosing birds. In at least the female choice experiment, however, acoustic signals seem unlikely to have influenced the results; male bearded tits do not use song or other vocalizations when defending or announcing territories (van den Elzen 1977). In an earlier study of bearded tits, Hoffmann (1994) found that female mate choice was more affected by morphology (beard length) than by male behaviour. In our study, stimulus and choosing birds were able to interact with each other in both the male and the female choice experiments. As any attempt to measure the response of either sex to tail length would be questionable without such interactions, we suggest that our results are best explained by mutual mate choice.

Our study thus shows that sexual selection may account for long tails in both males and females, but also that it seems to operate differently in the two sexes. In other words, female preference would drive tail elongation in males, whereas male mate choice rather results in stabilizing selection on female tail length. A review by Ryan and Keddy-Hector (1992) showed that when females show preference for traits that deviate from the population mean, they usually prefer exaggerated expressions of those traits. Therefore, our finding that female bearded tits preferred the male with the longest tail (regardless of absolute tail length) is not surprising, and it is also consistent with many other studies (reviewed by Andersson 1994).

The question is why males did not always prefer the female with the longest tail, i.e. why did they take absolute tail length into account? One possibility is that males actually prefer long-tailed females, but that male choice is more subtle than that of females and that our experimental set-up therefore failed to detect it. Alternatively, we suggest that a male may face a fitness trade-off when mated to a long-tailed female. Hoi and Hoi-Leitner (1997) found that clutch size was positively correlated with female body size and condition. As in this study tail length showed the highest factor loading (92%) among variables used for estimating body size (based on principle component analysis), tail length indicates female quality, i.e. fecundity, in bearded tits. If so, we would expect males to prefer long-tailed females (see Johnstone et al. 1996; Altmann 1997). In bearded tits, however, females decide where to build the nest. Moreover, attractive and high quality females prefer areas with high nest densities, where extra-pair fertilizations are frequent (Hoi and Hoi-Leitner 1997). As high quality females are also more likely to seek extra-pair copulations (Hoi 1997), a male mated with a long-tailed female may pay a cost in terms of lost paternity (see Reynolds and Côté 1995 for cost of female mate choice in redlip blennies *Ophioblennius atlanticus*). Therefore, it is not clear that males would always benefit from choosing long-tailed females as mates. If the costs are higher than the potential benefits, male mate choice in bearded tits may constrain tail elongation in females. Such stabilizing sexual selection has been found in several other species (e.g. Rowland 1995; Wollerman 1998).

Our results on male display behaviour suggest that male bearded tits follow a mixed reproductive strategy. Even if males preferred to spend more time with control than short-tailed females, they performed sexual displays towards both. Moreover, males seemed to adjust sexual display behaviour according to the time they spent with long-tailed females. Thus, even if males try to establish a pair bond by keeping contact with and closely following a female, they may solicit other females by using display behaviour. This double strategy could increase male mating success, including extra-pair copulations. A recent experiment supports that female tail length influences extra-pair behaviour in male bearded tits; males mated to a long-tailed (i.e. attractive) female were less likely to show courtship behaviour towards other females (Romero-Pujante 2000).

Direct sexual selection also includes intrasexual competition. During the fertile period, bearded tits frequently perform conspicuous chase-flights, which are often initiated by the female and attract neighbouring males. These flights may end in the female copulating with the winning male, not necessarily her social partner (Hoi 1997). Flight performance, and hence tail length, may therefore influence contest competition as well as mate choice (see Balmford et al. 2000). It is, however, difficult to predict whether tail length or some other trait is most important for successfully competing in the chase-flights performed by bearded tits.

We cannot rule out the possibility that long tails in female bearded tits have evolved as a by-product of direct sexual selection on males. The correlated response hypothesis has been proposed to explain tail length in female barn swallows *Hirundo rustica* (Cuervo et al. 1996), plumage coloration in female house finches *Carpodacus mexicanus* (Hill 1993), epaulet size in female red-winged blackbirds *Agelaius phoeniceus* (Muma and Weatherhead 1989) and plumage coloration and spottiness in barn owls (Roulin et al. 2001). Except for the barn owl (Roulin et al. 2001 and references therein), however, these studies did not find a relationship between the trait in question and female quality, as documented in the bearded tit (Hoi and Hoi-Leitner 1997). Furthermore, recent comparative studies suggest that female ornaments often have evolved independently of male showiness (reviewed by Amundsen 2000, but see Cuervo and Møller 2000).

To summarize, our results suggest that direct sexual selection may explain the presence of long tails in male and female bearded tits. Furthermore, sexual dimorphism in tail length may be because of different intensities of sexual selection in males and females. It remains to be clarified whether other factors (e.g. genetic correlation and natural selection) also have influenced the evolution of long tails in bearded tits.

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